

COMMENTS ON A REVISION OF *CELTIS* SUBGENUS *MERTENSIA* (CELTIDACEAE) AND THE RECOGNITION OF *CELTIS PALLIDA*

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ABSTRACT

In 2001 Berg and Dahlberg, in their revision of *Celtis* subgenus *Mertensia*, included the Spiny Hackberry (*Celtis pallida*) within the older named *Celtis ehrenbergiana* (type locality Querétaro, México). The type specimen of *C. ehrenbergiana*, with its single supranodal, curved thorn (not paired, straight, node-bearing thorns), domatia on both the primary and secondary vein axils (not restricted to the primary vein axils), and larger fruit pyrenes, is referable to the widespread *C. iguanaea*. *Celtis pallida* occurs both in the southwest USA-Mexico (type locality Texas) and in southern South America where it occurs with the closely related, but older-named *C. tala*. Characteristics exist to support separation of *C. tala* as a species distinct from *C. pallida*, thus mandating the use of the name *C. pallida* for the southwest North American Spiny Hackberry.

RESUMEN

En su revisión de *Celtis* subgénero *Mertensia*, Berg y Dahlberg (2001) incluyen al granjeno (*Celtis pallida*) dentro del concepto de la especie *Celtis ehrenbergiana* (localidad tipo Querétaro, México), la cual fue descrita con anterioridad. El ejemplar tipo de *C. ehrenbergiana*, con espinas solitarias, supranodales y recurvadas (no en pares, rectas y nodales), domacios en las axilas de las venas primarias y secundarias (no restringidos a las axilas de las venas primarias), y fruto con pirenos más grandes, es asignable a la especie de amplia distribución *C. iguanaea*. *Celtis pallida* habita tanto en el sureste de los Estados Unidos y México (localidad tipo Texas) como en el sur de Sudamérica donde crece con *C. tala*, una especie estrechamente relacionada y con nombre más antiguo. Existen varios caracteres que apoyan la separación de *C. tala* como especie distinta de *C. pallida* y, por lo tanto, este último nombre es el que debe aplicarse al granjeno del suroeste de Norteamérica.

INTRODUCTION

In a revision of *Celtis* subgenus *Mertensia*, Berg and Dahlberg (2001) placed the Spiny Hackberry, *Celtis pallida* Torr., within *Celtis ehrenbergiana* (Klotzsch) Liebm. The new name now occurs frequently on the World Wide Web, and has been accepted by the official U.S. Department of Agriculture "Plants" database (<http://plants.usda.gov/>) and is beginning to appear in the botanical literature. It is the intention of this paper to demonstrate that *Celtis ehrenbergiana* is a northern derivative of and synonym of the widespread *Celtis iguanaea* (Jacq.) Sarg. and is not conspecific with *C. pallida*. Also, *Celtis pallida* is recognized as a species distinct from the closely related *C. tala* Gilles ex Planch. of Argentina.

Most North American *Celtis* species belong to subgenus *Celtis*, which is characterized by two long, undivided styles per ovary, the absence of nodal thorns or spines, and the absence of domatia (small pocket-like flaps) in some vein axils on the abaxial leaf surfaces. This subgenus is represented in North America north of Mexico by *Celtis laevigata* Willd., *C. lindheimeri* K. Koch, *C. occidentalis* L., *C. reticulata* Torr., *C. tenuifolia* Nutt. (Sherman-Broyles et al. 1997). Subgenus *Mertensia* is largely neotropical, with species characterized by paired styles that are again divided below the tip (i.e., bifurcated styles), having solitary or paired thorns above the nodes, and domatia in the vein axils on the abaxial leaf surface.

Two species from subgenus *Mertensia* also occur in North America. *Celtis iguanaea* is a widespread species occurring in tropical areas from southern South America (Argentina) through Central America into central Mexico, and through much of the Caribbean and is reported from southern Florida in the U.S.D.A. Plants website but not in Flora North America (Sherman-Broyles et al. 1997). The second species is *Celtis pallida* and has an amphitropical distribution from the southwest United States (southeast Arizona, southern New

Mexico, trans-Pecos and south Texas) into central Mexico (Baja California Sur, Sonora, Sinaloa, Chihuahua, Coahuila, Durango, Zacatecas, San Luis Potosí, Nuevo León, Tamaulipas, Querétaro, Hidalgo, México, Veracruz, Puebla, Oaxaca, and Chiapas), also in Lee County, Florida, and in South America, in north-central Argentina and adjacent Paraguay (Hunziker & Dottori 1976).

In their revision of *Celtis* subgenus *Mertensia*, Berg and Dahlberg (2001) recognized six species, four restricted to dry or deciduous gallery forests in South America and two occurring in both North and South America. They recognized a very broad, variable and wide-ranging *C. iguanaea* that includes lianas, shrubs and small trees with leaves varying greatly in size, marginal toothiness and vestiture. They list 26 heterotypic synonyms for the species, but they recognize four peripheral variants as separate species based on differences in style branches (*C. loxensis* C.C. Berg), vestiture [*C. brasiliensis* (Gardner) Planch., *C. chichape* (Wedd.) Miq. in Mart.], and young-stem coloration (*C. orthocanthos* Planch.) as well as thorn structure etc. (Berg & Dahlberg 2001).

Berg and Dahlberg (2001) placed the more xeric shrubs with smaller leaves into *Celtis ehrenbergiana* (epithet named in 1847) listing 13 heterotypic synonyms of the species, including the South American *C. tala* (1848) and the amphitropically distributed *C. pallida* (1858). It is in this that I disagree with the authors.

CELTIS PALLIDA VS. CELTIS IGUANAEA

Celtis pallida is very different from *C. iguanaea*, differing in growth habit, the structure of the supranodal thorns, the distribution of domatia on the lower (abaxial) leaf surface, size and structure of the leaves, and the size of flowering styles, mature fruit and pyrenes.

Celtis pallida is an erect, much-branched shrub with notably zig-zagged stems; stem nodes usually produce a pair of straight, sharp-tipped, divergent, lignified thorns (1–)5–20(–55) mm long directly above the nodes. Thorns over 5(–10) mm long bear 1–3 nodes and the thorn nodes typically develop single or fasciculate leaves or even lateral branches. When the thorns are very long they can have secondary thorns above their axillary leaves and thus may mature into branches. But very short thorns can lack nodes, and thorns can sometimes be solitary above the nodes, and some branches can lack thorns altogether. The abaxial domatia are usually restricted to the lower midrib axils with the first pair of secondary veins, and the domatia may become swollen and green in color, and they also sometimes occur in the mid-leaf portion—there are none in the axils of the secondary to tertiary vein axils (except in occasionally very large leaves). Leaves range from entire to crenate-serrate, 10–25(–43) mm in length, 6.5–14(–33) mm in width. Inflorescences are small, axillary dichasial cymes consisting mostly of staminate flowers, with only 1–2 bisexual flowers. The two style bases are flattened, ± 1 mm long, to 0.7 mm wide, each producing two equally short, papillate divergent lobes at their tips with the papillae extending down the margins of the broad style bases. Mature fruits are orange, usually 6–7(–8) mm in diameter when dried and have a rounded, white pyrene to 4 mm long with a low, alveolate-reticulate sculpturing.

In contrast, *Celtis iguanaea* can be a tree or shrub with spreading liana-like branches or a liana that typically produces a solitary, sharp-tipped, decurved, woody thorn 2–8(–10) mm long above each node; these are rarely paired, rarely to 25 mm long and when large may rarely bear a leaf and secondary decurved thorn at the tip. Inflorescences often develop at the base of the thorn or from the stem below the thorn base and are considerably larger than those in *C. pallida*. Domatia are often poorly developed at the base of the midrib at the axils of the basal secondary veins, but they occur well up the midrib and also along the paired secondary veins in the outer axils with the tertiary veins (this however, may be a feature of leaf size). Leaves in tropical areas are often oblong, to 100–150 mm long, 45–60+ mm wide, pinnately veined above the base, with caudate tips, cuneate to subcordate bases, entire or crenate-serrate toothed margins, but in drier areas of Mexico they are more ovate to oblong-ovate, (15–)33–100 mm long, (10–)20–50(–85) mm wide, and can be well within the size range of those of *C. pallida*. Leaves can also become thick, coarse, strongly scabrous, and have fewer domatia in arid regions. Styles are similar in structure to those of *C. pallida*, but to 3–4.5 mm in total length. Mature fruit are orange to orange yellow, edible, 7–12 mm in diameter, and

when mature the rounded pyrene is white, 5–7 mm long, with irregularly raised margins around the coarse alveolate reticulations.

THE TYPE OF *CELTIS EHREBERGIANA*

Klotzsch (1847) cited a single collection by C. Ehrenberg in his description of *Momisia ehrenbergiana* Klotzsch, the basionym of *Celtis ehrenbergiana* (C. Ehrenberg 1114). The type collection was borrowed from the Berlin Herbarium (B) (Fig. 1). It has Ehrenberg's original label "Arbor seu frutex, ubique in loc. calid. las ajuntas (sic), Montezuma, Jan. 1840, Mexico, C. Ehrenberg 1114." (=Tree or shrub, common in warm sites...)

The las ajuntas noted is actually Los Adjuntos, a small mining settlement along the Río Montezuma that separates Querétaro from Hidalgo near a small contemporary village of Maconi, Querétaro, northwest of Zimapán, Hidalgo. The locale is shown on the 1937 map of Querétaro in the Atlas Geográfico de los Estados Unidos Mexicanos (Anonymous 1932–1937).

The type specimen of *C. ehrenbergiana* (Fig. 1) is rather sparse, consisting of two branches, no flowers, and one sub-mature fruit in the packet. The leaves are ovate, 27–57 mm long, 22–37 mm wide, rounded, or in one leaf, with an obtuse point at the tip, rounded at the base, subentire to crenate with up to 8 teeth, with veins impressed above, with the mid and secondary and some tertiary veins raised, brownish-yellow, the larger 0.3–0.5 mm wide beneath. The leaves are coarse and thickened (as seen in leaves over a year in age) the blades are hirtellous-hirsute and coarsely scabrous with hairs to 0.2–0.3 mm long (to 0.5 mm long along the leaf margins). There are domatia in the axils of the four secondary veins that branch from the base to upper-mid-section of the midrib, and between the secondary and larger tertiary veins on the abaxial leaf surface. The sub-mature dried fruit measured 10.2 × 8.7 mm, the immature pyrene is estimated to be ± 5 mm in diameter. Only one thorn can be seen on the specimen, this on the shorter branch, and it is solitary, strongly decurved, ± 3 mm long, but the tip has been broken off (Fig 1B).

The upper epidermis of the type of *C. ehrenbergiana* has a very bullate appearance in part due to the cystoliths, but the epidermal cells can be seen with 40× magnification and they have a distinctive radiating pattern from the base of the erect, stiff hairs. This pattern is not found on all specimens, particularly those with young, thin leaves, but I have found several other Mexican specimens with the same epidermal pattern. All of these specimens have been placed within *C. iguanaea* based on other characteristics, with the single curved thorn being the best character to distinguish the species from *C. pallida*.

The TEX-LL herbaria has many specimens of *Celtis* from central Mexico (Veracruz, México, Morelos, Hidalgo and San Luis Potosí) that have leaves of the same general size and shape, with crenate leaf margins, and that have curved non-node-bearing thorns, and large fruit like those of the type of *C. ehrenbergiana*. The type of *C. ehrenbergiana* is not an isolated specimen, rather is representative of populations of the drier portions of interior Mexico.

I visited the Los Adjuntos site in June of 2004 to collect the *Celtis* species in the area. The Los Adjuntos area has low xeric subtropical scrub, strongly disturbed fields, pastures and disturbed woodlands with *Acacia farnesiana*, *Mimosa* spp., *Neopringlea*, *Karwinskia*, *Colubrina*, *Vallesia glabra*, *Capparis incana*, *Maclura tinctoria*, etc. *Celtis pallida* (Henrickson 23639, TEX) was frequent in disturbed open areas. We then went back into the mountains and came down another road that crosses the Río Montezuma about 18 km to the south at Presa de Zimapán (which forms Laguna de Zimapán) on a road that leads to Zimapán, Hidalgo. Just east of the dam, we again found shrubs of *Celtis pallida* (Henrickson 23648, TEX) and further on a second species *Celtis caudata* Planch. (Henrickson 23645, TEX) of subgenus *Celtis*. No specimens similar to the type of *C. ehrenbergiana* were found on the trip. However, it can be stated that *C. pallida* near type locality of *C. ehrenbergiana* is characterized by paired nodal thorns bearing nodes, small leaves with domatia only along the midrib and other character-states typical of *C. pallida* elsewhere and it does not look anything like the type of *C. ehrenbergiana* near its type locality. On the other hand, the type of *C. ehrenbergiana* clearly must be considered a dryland phase of *C. iguanaea*, based on the diagnostic character-states shared with that species.

Therefore *Celtis ehrenbergiana* (Klotzsch) Liebm. 1851 (based on *Momisia ehrenbergiana* Klotzsch 1847)

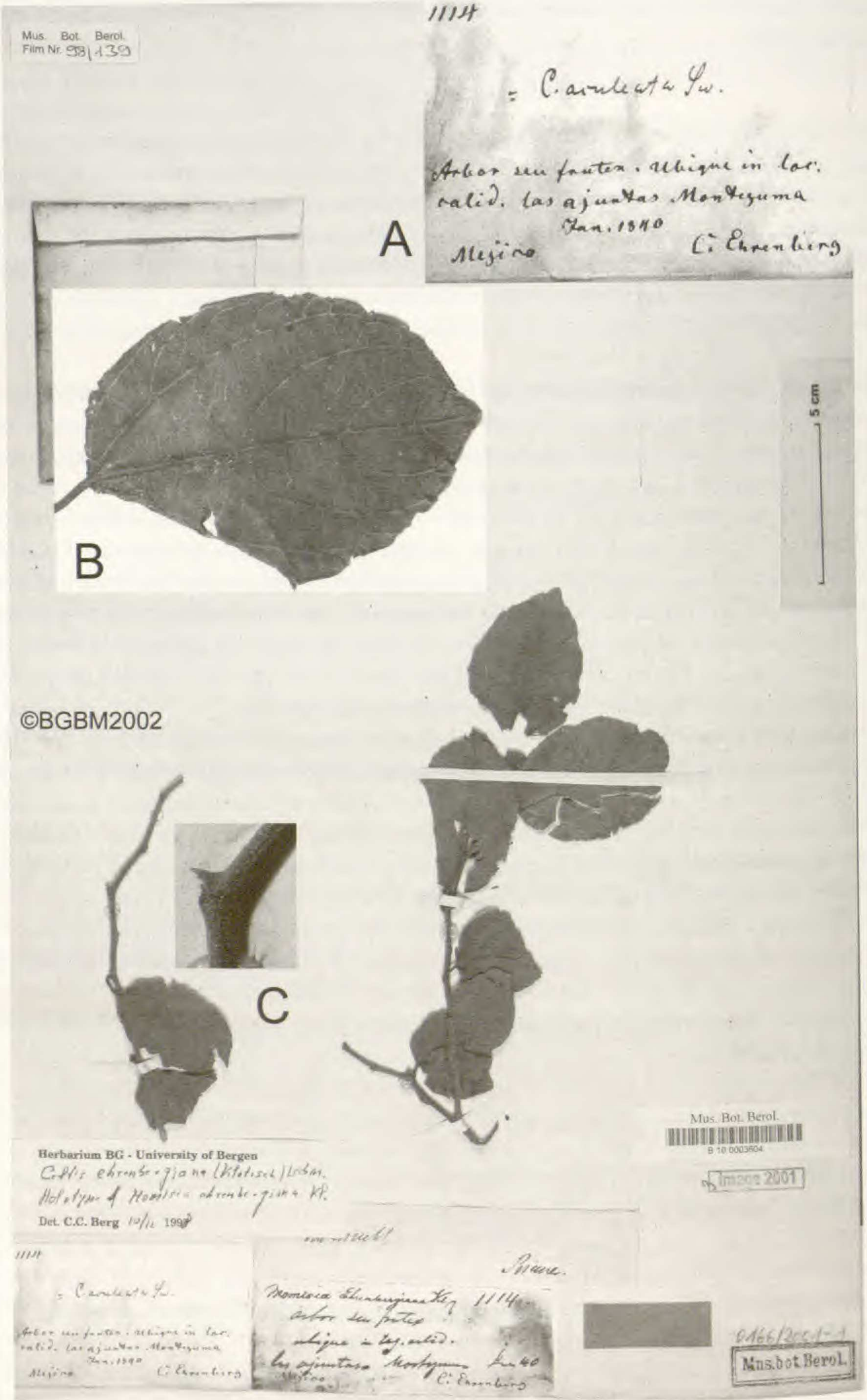


FIG. 1. Holotype specimen of *Celtis ehrenbergiana* (Klotzsch) Liebm., collected by C. Ehrenberg (no. 1114) from vicinity of the Río Monteuma, Querétaro, Mexico with overlays of specific materials. A. Enlargment of the label from the lower left hand corner of the specimen. B. Enlarged leaf from packet. C. Only one supra axial thorn remains on specimen on fragment to left, it is enlarged in C.

from collections from along the Río Montezuma, in Querétaro joins three other named species described from Mexico that are synonyms of *C. iguanaea* (Jacq.) Sarg. (1895) [based on *Rhamnus iguanaeus* Jacq. (1760)]. These include: *Mertensia laevigata* H.B.K. (1817) [= *C. laevigata* (H.B.K.) Spreng. non *C. laevigata* Willd. (1814)], from the state of Campeche; *C. anfractuosa* Liebm. (1851) from Veracruz; and *C. platycaulis* Greenm. (1903) from Morelos (see Berg & Dahlberg 2001).

CELTIS TALA VS. CELTIS PALLIDA

With the removal of *C. ehrenbergiana*, there remains in Berg and Dahlberg's *C. ehrenbergiana* two species that have been previously recognized as distinct: *Celtis tala* Gillies ex Planch. (described in 1848) and *C. pallida* (described in 1858) (Hunziker & Dottori 1976; Berg & Dahlberg 2001). If the two taxa were considered conspecific as treated by Berg and Dahlberg (2001), then *C. tala* would be the oldest available name for the taxon. So I present here a brief analysis of these two species.

Celtis pallida, as noted above, occurs both in North America and in South America in northern Argentina and adjacent Paraguay. *Celtis tala* is confined to north and east Argentina, and adjacent southern Uruguay, and south Brazil (Hunziker & Dottori 1976; Romanczuk & Martínez 1978; Dottori & Hunziker 1994).

Taxonomic history.—Sprengel (1825) in the 16th [17th] edition of Linneaus' *Systema Vegetabilium*, described a *Celtis spinosa* Sprengel from Brazil (location unknown) characterized by flexuous stems and paired curved spines.

Planchon (1848) described *Celtis tala* (spines paired, straight, leaves small, serrate to subentire) from Argentina. Here he also listed Sprengel's *C. spinosa* in his "Species non satis nota" with a notation complaining that the weak diagnosis was not instructive and that the taxon was perhaps better ignored.

In his later treatment in DeCandolle's *Prodromus*, Planchon (1873) once again ignored Sprengel's *C. spinosa*, but recognized five varieties of *C. tala* that differed in leaf shape and serration, young stem and leaf vestiture, and thorn number and shape. His var. *gilliesiana* of Argentina and Paraguay was considered the type variety (*vel typica*), var. *weddelliana* and var. *gaudichaudiana* were from Brazil, var. *chichape* from Bolivia, and var. *pallida* from Texas and Mexico.

Baehni (1937) resurrected Sprengel's *C. spinosa* and placed the later-described *C. tala* within *C. spinosa* in his treatment of South American *Celtis*. He also recognized Planchon's var. *weddelliana* as a variety of *C. spinosa*. Baehni's treatment was followed by Cabrera (1945), Digilio and Legnane (1966) and Dawson (1967) in their various flora treatments. This also led to M.C. Johnston (1957) making the combination *C. spinosa* var. *pallida* (Torr). M.C. Johnston for North American material.

Romanczuk (May 1976) in her study of Argentinian *Celtis*, rejected Baehni's concept of *C. spinosa*, reinstated *C. tala* as a species, but recognized a second species with paired, straight node-bearing spines as *C. weddelliana* (Planch.) Romanczuk. She further recognized a third species, *C. sericea* Romanczuk, differing from her *C. weddelliana* in having broader, crenate leaves, with the lower surfaces velutinous-sericeous (vs. having entire, ovate to narrowly ovate leaves with lower surfaces \pm uniformly pubescent). Lectotypes and holotypes were designated for these taxa.

Hunziker and Dottori (June 1976) also rejected the use of *C. spinosa*, showing it was attributable to *C. iguanaea*. They restored the names *C. tala* and *C. pallida* and presented complete synonymy and typified many of the synonyms, and in a post script (after having seen Romanczuk's 1976 paper) took Romanczuk (1976) to task for her typifications. They also listed all collections seen from North and South America. They demonstrated the value of pyrene characters for distinguishing *C. pallida* from *C. tala*, with *C. pallida* having a low reticulate sculpturing, vs. a much higher and variably raised reticulate sculpturing for the pyrenes of *C. tala* and provide pyrene illustrations of both taxa. They also noted that the only difference found between North and South American *C. pallida* taxa involved pyrene size with the North American plants having slightly larger pyrenes ($3.3\text{--}4.8 \times 2.6\text{--}3.8$ mm) than those in Argentina [$(2.4\text{--})2.9\text{--}3.8 \times (2\text{--})2.4\text{--}3.4$ mm]. In addition they described a new variety, *C. pallida* var. *discolor* Hunziker & Dottori, that differed from the nominal variety in having bicolored leaves, green and sparsely pilose above and whitish and densely sericeous beneath, and with vein axils having small to very small domatia. In their postscript they retypified

Romanczuk's *C. weddelliana*, noting that it corresponded to their *C. pallida* var. *pallida*, and they equated their *C. pallida* var. *discolor* to Romanczuk's *C. sericea*. Dottori (1976), in a separate paper, contrasted foliar morphology of *C. tala* and *C. pallida*, with special reference to the domatia.

In 1978 Romanczuk and Martinez presented a treatment of *Celtis* of Argentina, recognizing 6 species including *C. tala* and *C. pallida*, the latter with subsp. *pallida* and subsp. *sericea* (here using their epithet at the rank of subspecies rather than Hunziker's var. *discolor*). They presented data on pollen stainability for the six species of Argentina. They also presented phytochemical data obtained from two-dimensional paper chromatography of secondary compounds obtained from dried herbarium specimens using standard butanol-acetic acid-water (6:1:2) vs. 2 % acetic acid runs. Data were given as R.f. values in BAW vs. acetic acid runs, and the color of the spots in U.V. light vs. U.V. light in the presence of ammonia. While the specific compounds corresponding to these spots were not identified, *C. tala* and *C. pallida* gave different patterns of spots, while *C. iguanaea*, *C. spinosa* and *C. pubescens* gave almost identical patterns. The Argentina specimens of *C. pallida* were distinctive, but the signatures of subsp. *sericea* from Argentina were quite similar to those of North American subsp. *pallida*. Romanczuk (1987) also contributed the treatment of *Celtis* to the *Flora Illustrada de Entre Rios (Argentina)* where she used the name *C. pallida* subsp. *sericea*.

In summary, *C. tala* and *C. pallida* are closely related and share certain characteristics: (1) paired, straight, divergent, supranodal thorns; (2) relatively small, ovate to narrow, entire or distally weakly serrate-dentate leaves with three prominent basal veins and a gap between these and the more distal pinnate secondary veins; (3) domatia mainly occurring along the base of the leaf between the primary-secondary vein axils but also sometimes more distally along the midvein; (4) leaf epidermal cells with striate cuticles (Romanczuk & Martinez 1978); (5) and small glomerate inflorescences consisting mostly of staminate flowers, with few bisexual flowers. There are also consistent differences between the species as indicated in the following key modified from Hunziker and Dottori (1976) and following the nomenclature accepted in the *Catálogo de las Plantas Vasculares de la República Argentina II* (Zuloaga & Morrone 1999) and used in Dottori and Hunziker (1994).

1. Thorns paired, straight, bearing nodes and leaves, (6-)15-35(-46) mm long [but some shorter thorns (1.4-) 2-5(-12) mm long lacking nodes]; pyrenes generally (2.4-)2.9-4.8 mm long, (2-)2.4-3.8 mm wide, superficially reticulate (rarely smooth), the reticulae low, flat surfaced; _____ ***Celtis pallida***
2. Leaves concolorous, hairs few above, more common below, or the hairs common on both surfaces and then large and erect (none appressed); basal leaf domatia large, inflated; shrubs (1-)1.5-2.5(-3.5) m tall, 5-12 cm in basal diameter; sw. United States and Mexico; n.-cent. Argentina, rare in adjacent Paraguay. _____ ***Celtis pallida* var. *pallida***
2. Leaves generally bicolored, with a dense whitish indument of short appressed hairs on the lower surface, upper leaf surface with few hairs or glabrescent; basal leaf domatia small, sometimes inconspicuous; shrubs to small trees 1.4-5 m tall, 8-15 cm in basal diameter; n. Argentina. _____ ***Celtis pallida* var. *discolor***
1. Thorns paired, straight, lacking nodes and leaves, (1.5-)3-15(-20) mm long, (nodes sometimes present on sucker shoots); pyrenes (3.6-)4.8-5.8(-6) mm long, 3-5(-5.6) mm wide, the reticulae surfaces irregularly raised; trees (3-)4-8(-10)[-20] m tall, with trunks 3-6(-10) dm in basal diameter; s. Brazil, s. Uruguay, n.-central Argentina. _____ ***Celtis tala***

As the above key shows, *Celtis pallida* is a shrub-small tree 1.5-5 m tall with basal trunks 3-15 dm in diameter, the paired nodal thorns bear nodes and leaves, the fruit pyrenes are 2.4-4.8 × 2-3.8 mm in size, and the pyrene surface is marked with a low flat-surfaced reticulation. In contrast *Celtis tala* grows to be a large tree 4-10(-20) m in height with basal trunks 3-6(-10) dm in diameter; the paired nodal thorns do not form nodes and leaves, and the fruit pyrenes are slightly larger, 3.6-6.0 × 3.0-5.6 mm, with the reticulate patterns irregularly raised (see comparative illustrations in Hunziker and Dottori (1976), Romanczuk and Martinez (1978), Burkart (1987). But the problem with these species is the variation found in leaf size, outline, toothing, and the development of thorns. In Texas-Mexico *C. pallida*, leaf and thorn size varies greatly, along with leaf indentation, vestiture (sericeous, hirtellous to glabrous) and in well developed long shoots the paired supranodal thorns are well developed, with conspicuous nodes on the thorns but in other collections or branches of the same specimen thorns are highly reduced, often unequal in size, and without

nodes. If one looks only at the vegetative aspects of *C. pallida* vs. *C. tala*, they appear to blend together. But, the pyrene differences are consistent. And the trends in thorn nodes are real.

The above shows that there are differences between *C. tala* and *C. pallida* that have been used by Argentinean botanists to recognize the taxa as separate species and they were so recognized in the latest published catalogue of the vascular plants of Argentina (Zuloaga & Morrone 1999), though in most recent unpublished enumeration of the flora obtained from the Instituto de Botánica Darwinion the above taxa are all placed within *C. ehrenbergiana* following Berg and Dahlberg (2001).

In contrast to the paper of Berg and Dahlberg (2001), I conclude that *C. ehrenbergiana* should be considered a northern-most representative and a synonym of the widespread *C. iguanaea* (Jacq.) Sarg. and not related to the *C. tala-pallida* complex. Furthermore, based on the characteristics expressed by Hunziker and Dottori (1976) noted in the above key, I support the recognition of *C. tala* and *C. pallida* as distinct species. All the North American material should be referred to as *Celtis pallida* Torr. var. *pallida* in deference to the recognition of the South American *C. pallida* var. *discolor* and var. *pallida*. Of course, the one South American taxon can also be recognized as *C. pallida* subsp. *sericea* Romanczuk vs. *C. pallida* subsp. *pallida*. I also feel that the final disposition of *C. tala* vs. *C. pallida* and its varieties should involve a thorough molecular study and/or be made by botanists with extensive field experience in Argentina and not by botanists without first-hand knowledge of the taxa.

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